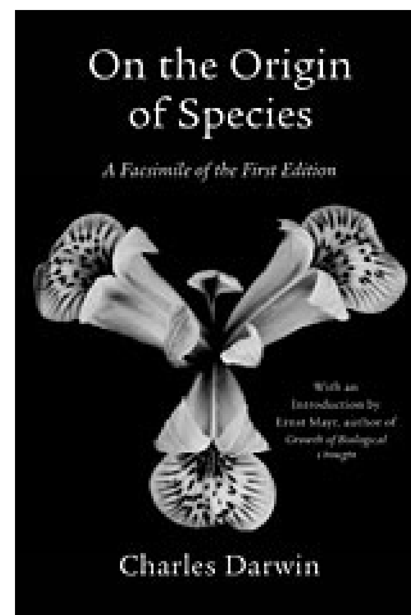
Evolutionary Aspects of Population Ecology

- Why do populations have the characteristics and rates they do?
- How can knowledge of these rates help predict the response of populations to changing conditions?



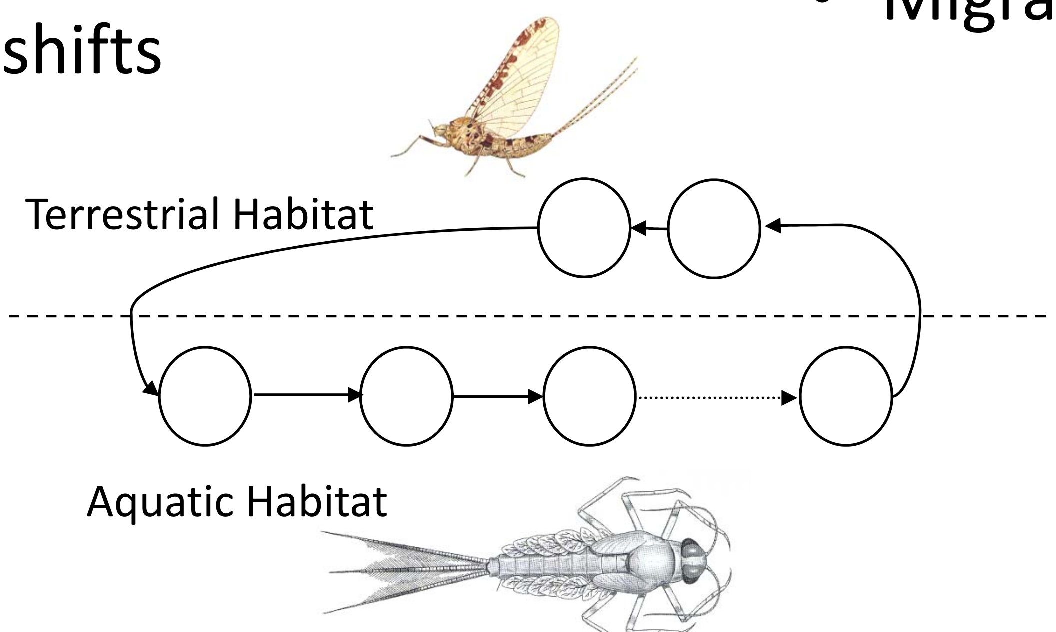
Evolutionary Aspects

- Evolution occurs over long time scales
- Management action occurs over much shorter ("ecological") time scales

- Often need to make decisions with little specific data. Knowledge of a species life history can help bound possibilities

Life history traits and demographic rates are product evolutionary history

- Iteroparity (one-time reproduction) vs. semelparity (repeat breeder)
- Metamorphosis; niche shifts
- Fecundity
- Age at first reproduction
- Parental care
- Migration/Anadromy



Life history traits

- May differ between closely related species
  - Semelparity vs. iteroparity in salmonids
- Among populations of the same species
  - Anadromy in *O. mykiss*:
    - Rainbow trout (resident freshwater)
    - Steelhead (sea-run rainbow trout)
- or even among individuals in the same population
    - Anadromy: residual steelhead
    - Age at 1st reproduction: early return by “jacks”

Evolutionary strategies

Evolutionary strategies

- Robert Mac Arthur and Ed Wilson (1967) suggested in their pioneering work on Island Biogeography that:
  - On arrival to an island "in an environment with no crowding (r selection) genotypes which harvest the most food will be most fit..." whereas
  - "in a crowded area (K selection), genotypes which can at least replace themselves with a small family at the lowest food level will win."

Evolutionary strategies

- Pianka (1970) expanded on these ideas and suggested species fall on a **continuum** with two endpoints:
- **r selected**
  - Rapid development
  - Early reproduction
  - small body size
  - semelparity (annual)

K selected

-slow development

-late reproduction

-large body size

-iteroparity (perennial)

Life history “decisions”

- At the beginning of any given breeding season, an individual must make several “decisions” with the goal of maximizing:

$$\lambda = S\ f$$

where S = survival rate

and f = fecundity

Life history "decisions"

- First decision: Breed?
  - Age at first reproduction
    - Size and fecundity
    - Grow and become more fecund, but risk death & no fitness?
      - pre-reproductive mortality stronger selective force than post-breeding mortality
    - May differ by species, sex, population
    - May differ through time

Life history “decisions”

- – If breeding, how much effort?
- – Reproductive effort:
  - • RE is the resources consumed during reproduction
    - – propagules
    - – migration
    - – parental care
  - • RE = total weight of propagules / Total biomass at maturity

  = gonadosomatic index (GSI)
- – High RE reduces parental survival (Roff 1992: 116)
- – Expend all (semelparity) or only some (iteroparity)?

Life history “decisions”

- Reproductive effort divided among
  - Offspring number and offspring size
    - Many small eggs vs. a few big eggs
  - Parental care: Yes?, No?, if so, How much?
    - Pre-breeding: redd building by salmon, egg size, content in fishes
    - Post-breeding: feeding of nestlings
  - Number of broods per season

Three example life history decisions

- Under what circumstances will fitness be maximized by the devotion of so much effort during first reproductive event that death ensues (semelparity)?

- Factors affecting clutch size in birds

- Evolution of diadromy in fishes

Semelparity vs. Iteroparity

- Annual vs. perennial plants
- Varies among species and populations of fishes:
  - Salmonids
  - American shad of east coast U.S. (Glebe and Leggett 1981)
  - coastal vs. interior populations of steelhead
- What happens when we alter the costs of reproduction and RE?

Semelparity vs. Iteroparity

- Cole (1954) asked the question: *what effect does repeated reproduction have on* r*?*
- <u>Life table analysis</u>

Semelparity vs. Iteroparity

- Cole (1954) concluded that the maximum gain for switching to iteroparity is equivalent to adding one individual to the average brood size for the semelparous case.
- In other words, annual with single brood of 101 has equal fitness as perennial with multiple broods of 100!
- Why? Even in best case (perfect survival after reproduction), older perennial individuals are contributing not much more than offspring of annual.

Semelparity vs. Iteroparity

- But most species are iteroparous! Why?

Semelparity vs. Iteroparity

- But most species are iteroparous! Why?
- Unrealistic assumptions:
  - Constant conditions

Semelparity vs. Iteroparity

- But most species are iteroparous! Why?
- Unrealistic assumptions:
- – Constant conditions
- – No cost to reproduction—survival was not linked to fecundity
- – Nonetheless, very useful model for understanding how fitness changes with reproduction schedule:
- – Reproductive value = V_x = How much is an individual of a given age worth in terms of future offspring.
  - When is V_x highest?

Semelparity vs. Iteroparity

- Semelparity is favored
  - when reproductive success increases *only* when RE is high **(Pacific salmon?)** or
  - when mortality in reproductive stages is high compared to juvenile stages (American shad, mayflies)

Semelparity vs. Iteroparity

- Semelparity is favored
  - when reproductive success increases *only* when RE is high **(Pacific salmon?)** or
  - when mortality in reproductive stages is high compared to juvenile stages (American shad, mayflies)
- Iteroparity is favored when
  - reproductive success is relatively high at low RE or
  - when survival rates in juveniles are poor and/or unpredictable compared to adult stages

American shad

- Leggett and Carscadden (1978) and Glebe and Leggett (1981) compared life history traits of populations of American shad along east coast of North America.
- All adults share the same ocean habitat (Gulf Stream)
- Observed strong differences in life history:
  - Connecticut River, CT
  - York River, VA
  - St. John’s River, FL

American shad

- At the time of river entry, gonadosomatic index (GSI) was higher in Connecticut River than St. John’s River, but eggs/mass higher for St. John’s females.
  - In CT population, all ova were mature at river entry
  - ~25% of somatic energy reserves transferred to eggs in FL population during upstream migration
  - Total energy / egg was similar
  - Timing of development and energy allocation differed between populations

American shad

- Latitudinal pattern:

Population	% Repeat Spawn	% Energy Consumed
New Brunswick	70%	--
Connecticut	35%	40-60%
York River, VA	25%	30%
St. John’s R., FL	0%	70-80%

Glebe and Leggett 1981

American shad

- What factors explain the latitudinal gradient?
- Proximate: Energetics during migration and reproduction:
  - Northern populations: 40% upstream migration, + 0% egg development + 15% outmigration = 55%
  - Southern populations: 50% upstream migration + 0% outmigration (died) + 30% gonad growth = 80%

American shad

- What factors explain the latitudinal gradient?
- <u>Ultimate?:</u>
- Temperature—warmer in FL = higher metabolic rates? Simply a population at edge of range?

American shad

- What factors explain the latitudinal gradient?
- <u>Ultimate?:</u>
- Temperature—warmer in FL = higher metabolic rates and costs of migration
- Predictability in spring warming, run-off, and food supply higher in Florida than New England ~ safer to put all the eggs in one basket…

General rule for fishes?

- Glebe and Leggett (1981) suggested that when adults expend more than a threshold value (~70%) of their energetic reserves during migration and spawning, the population is semelparous (Figure 13 of Glebe and Leggett 1981)

Lack 1966, 1968

- Reproductive rate depends on:
  – Number of eggs laid / clutch
  – Number of clutches laid / year
  – Age at first reproduction
- Clutch size
  – Increases during high food conditions (Cody 1966)
  – Increases with lattitude

- Many species have a characteristic clutch size:
  - Petrel = 1
  - Pigeon = 2
  - Gull = 3
  - Duck = 7-12
  - Partridge = 10-20
- Why have a specific clutch size?
  - Why not a larger clutch size?

1) Mechanical / physiological constraints

- Only so many eggs can be produced inside body the cavity or with available resources
- Does the observed clutch size reflect mechanical/physiological constraints?
  - How could we test?

1) Mechanical / physiological constraints

- Only so many eggs can be produced inside body the cavity or with available resources

- Does the observed clutch size reflect mechanical/physiological constraints?
  - How could we test (for indeterminate layers)?
    - Remove eggs—does female lay more eggs?

2) Incubation

- Clutch size is limited by number of eggs the sitting bird can cover

3) Mortality

- Past mortality during rearing (natural selection) has adjusted the clutch size to maximize the number of offspring—clutches that were too large were selected against

4) Food

- In most birds, clutch-size has evolved through natural selection to correspond with the largest number of young for which the parents can, on the average, find food.

Food to nestlings

- House Wrens
- Brood size

Brood size	Trips	Trips/Nestling
1	115	115
2	156	78
3	198	66
4	236	59
5	270	54
6	300	50

The Lack value

- The Lack value (the clutch size that produces the largest number of offspring) is probably incorrect for at least two reasons:

The Lack value

- The Lack value (the clutch size that produces the largest number of offspring) is probably incorrect for at least two reasons:
  - Effects of large clutch size on parent survival or future fecundity

The Lack value

- The Lack value (the clutch size that produces the largest number of offspring) is probably incorrect for at least two reasons:
  - Effects of large clutch size on parent survival or future fecundity
  - Environmental variability

Evolution of diadromous migration in fishes

- Diadromy-use of ocean and freshwater
- Anadromy-freshwater reproduction, ocean feeding
- Catadromy-ocean reproduction, freshwater feeding
- Remember: $\lambda = S\ f$

Evolution of diadromous migration in fishes

- Diadromy-use of ocean and freshwater
- Anadromy-freshwater reproduction, ocean feeding
- Catadromy-ocean reproduction, freshwater feeding
- Remember: $\lambda = S\ f$

$$= (S_{FW}\ S_{ocean})\ (f_{FW} + f_{ocean})$$

Evolution of diadromous migration in fishes

- Remember: $\lambda = S\ f$

$$= (S_{FW}\ S_{ocean})\ (f_{FW} + f_{ocean})$$

assume f ~ growth

S_{FW} / S_{ocean} in early life history stages determines where to spawn

f_{FW} / f_{ocean} determines where to feed

Evolution of diadromous migration in fishes

S_{FW} / S_{ocean} in early life history stages determines where to spawn

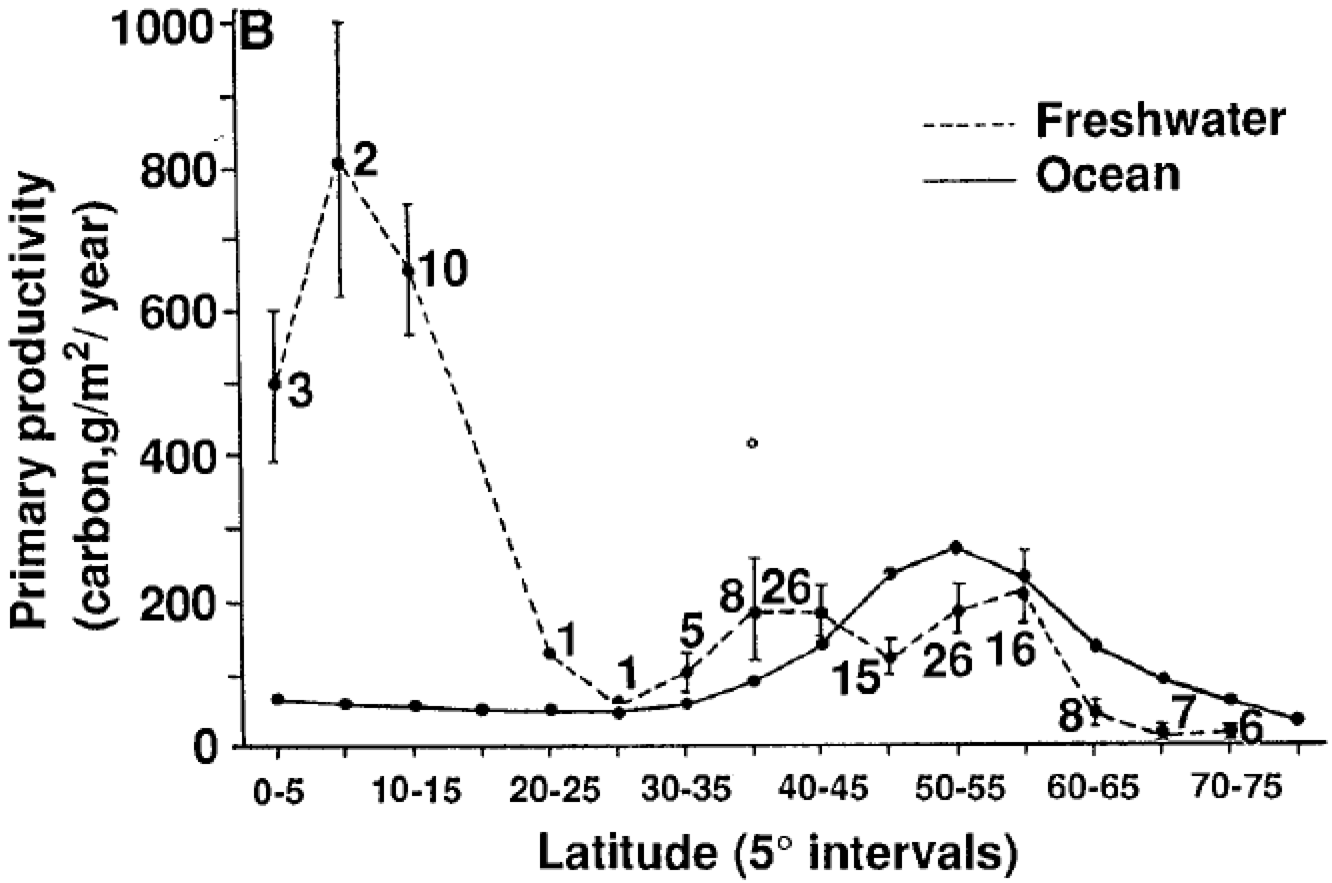
f_{FW} / f_{ocean} determines where to feed

Predictions? Salmon

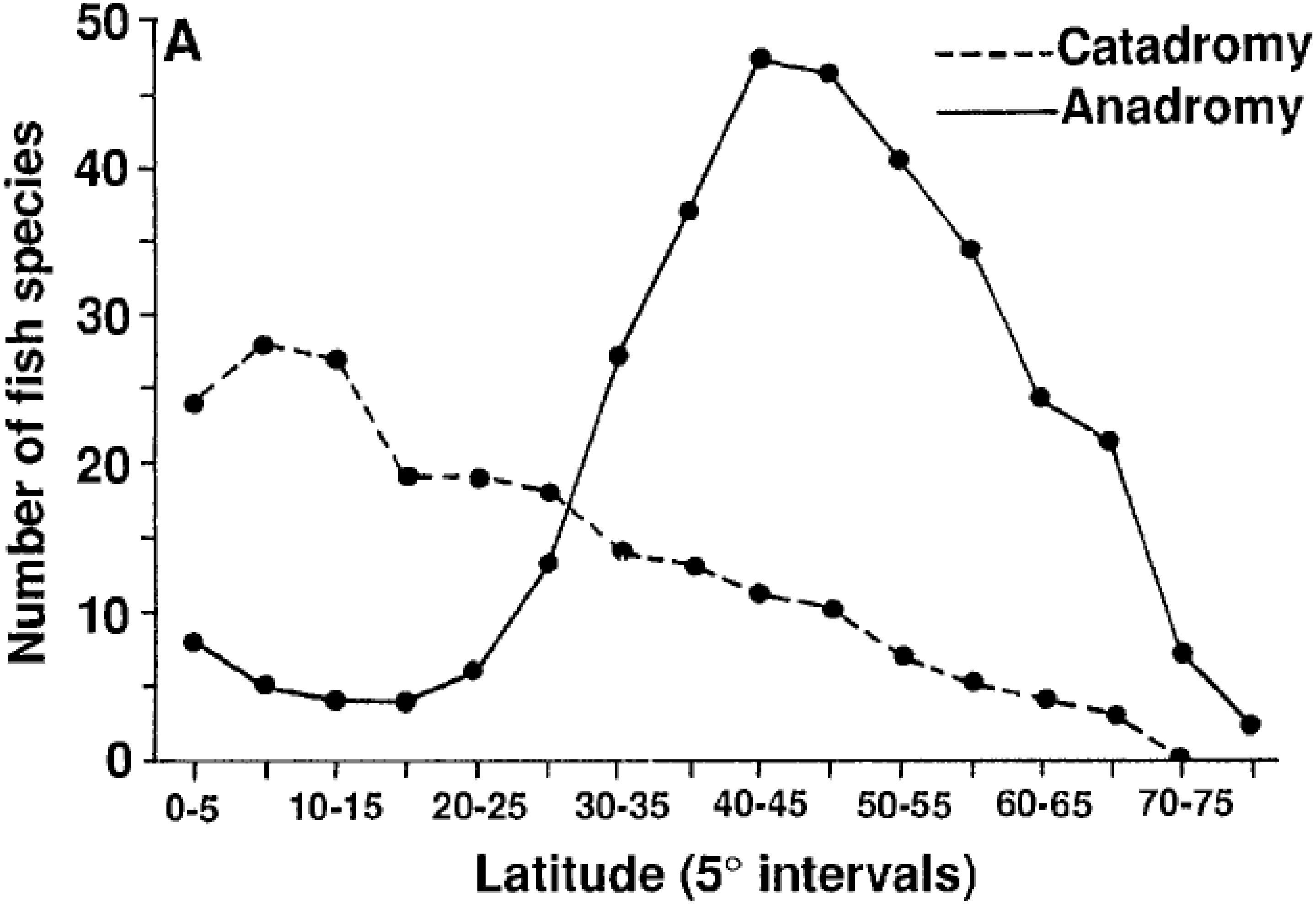
Eels

What data could we collect to test?

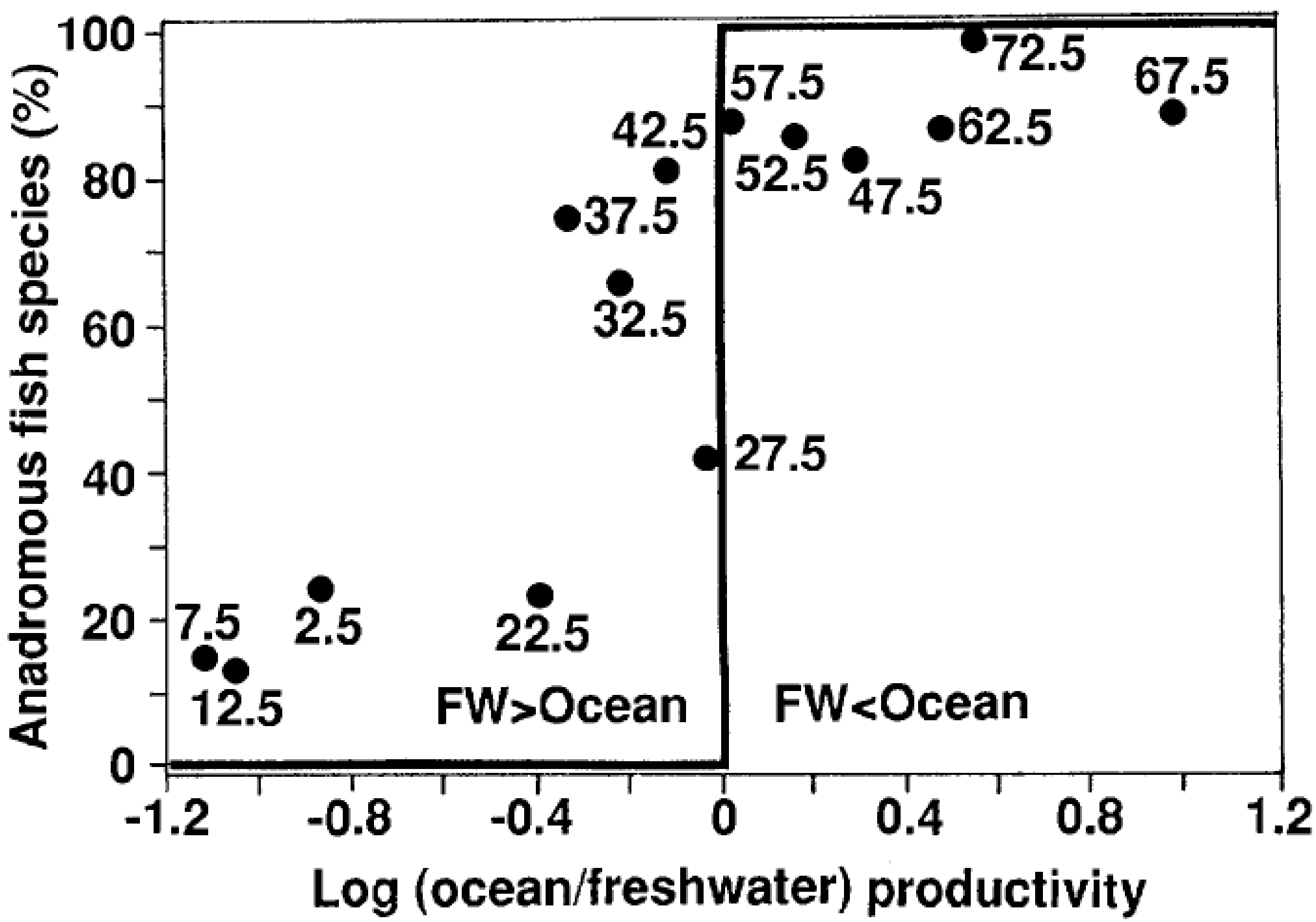
Gross et al. (1988)



Gross et al. (1988)



Gross et al. (1988)



Summary

- Evolution (and ecology) shape the life histories of species, populations, and individuals
- Life history theory can help clarify which selective forces may have been important in the past *and*
- Which selective forces could have the greatest effect in the future

Summary

- Can use life history theory to understand potential future conditions
  - Increased energetic costs during migration?
  - Increased food supply during nesting period?